Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance

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Manuscript received April 1998; accepted February 1999

Abstract

Ocean currents operating near the reef front at Ningaloo were studied by direct observation, aerial surveys (1990-92), and a current drogue, demonstrating a predominent northward current along the reef front during late summer and early autumn. It is proposed that this current be termed the "Ningaloo Current". Satellite sea surface temperature images show that this Ningaloo current is in fact the dominant current on the inner shelf from September to mid-April each year, and is a counter-current to the southward Leeuwin Current further offshore at the shelf break. The satellite imagery and current drogue data demonstrated how these opposing currents generate a recirculation of water in the region. The Ningaloo counter-current may determine the dispersal of coral larvae following the autumnal mass reef spawning. The circulatory movement may also be important in retaining planktonic biomass within the Ningaloo ecosystem, and is probably responsible for the extremely active food chain at this time of year and the presence of whale sharks. It may also, through natural selection, influence the timing of spawning of corals and other invertebrates on the reef.

Introduction

The dominant current off the west coast of continents throughout the world is an equatorward cold current forming the eastern limb of the subtropical gyres. In the south-eastern Indian Ocean, this current is generally depicted as a cool West Australian Current flowing northwards, but it is now known that the boundary current off Western Australia is in fact the warm poleward-flowing Leeuwin Current (Cresswell & Golding 1980; Godfrey & Ridgway 1985; Pearce 1991).

The Leeuwin Current is a stream of low salinity, warm tropical water that maintains the waters of the west coast of Australia at temperatures suitable for coral growth, and is thought to help sustain the extensive coral reefs that are found at Ningaloo Reef and the Houtman Abrolhos Islands about 29 °C (Hatcher 1991). It flows most strongly during the autumn, winter and early spring months, and has an important influence on many biological processes along the coast (Cresswell 1991; Phillips *et al.* 1991; Hutchins 1991; Hutchins & Pearce 1994). Both satellite imagery (A F Pearce, CSIRO Marine Research, Perth, unpublished data) and ship-borne observations (Thompson 1984) indicate that the Leeuwin Current is often narrow and comparatively close to shore off the Ningaloo Reef where the continental shelf is very narrow (Fig 1).

Ningaloo Reef stretches some 260 km south from North-West Cape (Fig 1), and is the only extensive coral reef in the world fringing the west coast of a continent. The distance offshore averages only 2.5 km, varying from only about 200 m to 7 km (R F May, National Parks

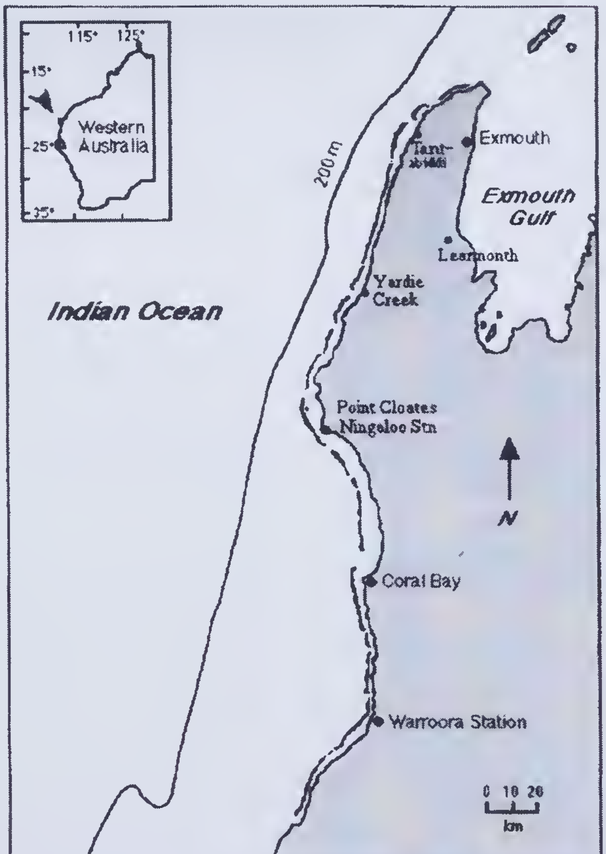

Figure 1. The Ningaloo Reef stretches 260 km along the west coast of the North-West Cape. The location in Western Australia is shown (inset). The dashed line indicates the approximate position of the 200 m. contour, on the edge of the Continental shelf.

Authority, personal communication) and partially enclosing a coastal lagoon between 1 and 2.5 m deep at low spring tide. Hearn & Parker (1988) have estimated that the gaps in the northern portion of the reef comprise some 15% of the length.

The continental shelf break in the northern reef at Ningaloo is at a depth of about 100 m and is only 6 to 10 km offshore; this is the narrowest part of the shelf in Australia. The coastline veers sharply eastwards, south of Point Cloates (Fig 1), and the width of the shelf (100 m contour) increases to over 30 km. On this wider shelf, the shelf break is not very strongly defined compared to further north where a number of steeply shelving underwater canyons are a feature.

Studies of the lagoon sea temperature and tide in the Ningaloo reef system (Simpson & Masini 1986) showed that the tides were semi-diurnal, with spring and neap tides occurring 2-4 days and 8-10 days respectively after a full or new moon. They found considerable diel variation in temperature, the range averaging 3 °C. There was a good correlation between measured temperatures and those determined by satellite imagery. Occasional temperature anomalies were noted, involving a sharp drop in temperature of 1 to 2 °C below seasonal values for 2 to 3 days, usually during neap tides.

In an extensive review of oceanographic processes in this area, Hearn *et al.* (1986) explored various scenarios that might cause these temperature anomalies, the arrival of a body of colder water, upwelling off the Ningaloo Reef, or large internal waves. They concluded that the fall in temperature is probably caused by upwelling associated with internal wave activity. Measurements of the circulation across and around the reefs indicated that water transported shorewards across the reef by wave and swell action tends to flow along the lagoon and out at the ends (mainly towards the south). The residence time of water within the lagoon system is a matter of hours (Hearn & Parker 1988).

Water circulation on fringing reefs has been extensively studied in Guam (Marsh *et al.* 1981). Under normal conditions, water entering the lagoon over the reef finds its way to adjacent gaps where it flows back out to the ocean. The flow in the gaps only reverses in conditions of a strong rising tide. Observations at Ningaloo show a similar current system (Hearn *et al.* 1986).

Studies further south along the Western Australian coast have demonstrated that there are inshore, wind-driven, northward counter-currents to the Leeuwin current near the Abrolhos Islands (29° S; Cresswell *et al.* 1989; Pearce 1997) as well as between Cape Leeuwin and Cape Naturaliste (34° S) from November to March each year (Pearce & Pattiaratchi 1999).

The scleractinian corals of the west coast of Australia reproduce each year in mass spawning events following the March and April full moons (Simpson 1985, 1991; Simpson & Masini 1986). The coral planula takes over 7 days to develop to a stage where settlement may occur and is dispersed by ocean currents. Theories regarding coral spawn dispersal at Ningaloo have hitherto assumed that spawn is dispersed southwards by the Leeuwin Current, which intensifies at this time of year. A unidirectional gene flow between separate coral reefs in Western Australia has been proposed (Simpson 1991).

We describe here surface currents on the continental shelf off Ningaloo between 1987 and 1992 using direct observation of current plumes, from boats, and aerial surveys (conducted for whale sharks, 1990 to 1992) and data from a current drogue. Confirmatory data were derived from satellite imagery (1991 to 1996) to confirm the existence of a seasonal inshore northwards counter-current.

Methods

No contemporary weather records for the Ningaloo Reef are available; the nearest station at Learmonth (Fig 1) is in the wind shadow of the Cape Range and therefore has somewhat different conditions from the west coast. Monthly wind rose data from a discontinued weather station at Cape Cuvier (24° S, immediately to the south of Ningaloo Reef) have been analysed to show seasonal variations in wind strength and direction.

Coral spawning events were personally observed on many occasions from boats at Bundegi Reef (north of the Exmouth township) in Exmouth Gulf and at Tantabiddi Reef and Coral Bay on the west coast (Fig 1). These data were supplemented with observations made by other divers, from other locations whenever possible (Table 1).

Table 1

Dates of confirmed coral spawnings, 1984 to 1996.

YEAR	MARCH	APRIL	COMMENTS
1984	25-26		Simpson (1985)
1985	15-16		Simpson (1985)
1986	3-4		
1987	21-23 *		
1988	10-12 *	9-10 *	
1989	29-30 *		
1990	18-19 *		
1991	9-10 *	7-8 *	
1992	26-27 *	24-25 *	
1993	16-17	15 *	
1994		3-4 *	
1995	25-26		
1996	14-15	10-13	Cyclone Olivia

* denotes spawning events directly observed by the authors; all other events verified by divers monitoring spawning at Exmouth and Coral Bay.

Preliminary direct observations of currents along the reef commenced in 1987. Although most of the water transport in the lagoons is parallel to the reef front (Hearn & Parker 1988), turbid water flows out of the lagoon through the major gaps in the reef and turns in the direction of the prevailing alongshore current. The boundary between the turbid lagoon water and the clear water offshore of the reef front can be clearly seen from boats and particularly from planes overhead, often extending over 500 m offshore (Fig 2). This phenomenon allows determination of the reef front current direction both from surface vessels and from aircraft.

Between 1990 and 1992, regular aerial surveys for whale sharks were conducted along the Ningaloo Reef from February to May using a single-engined Cessna

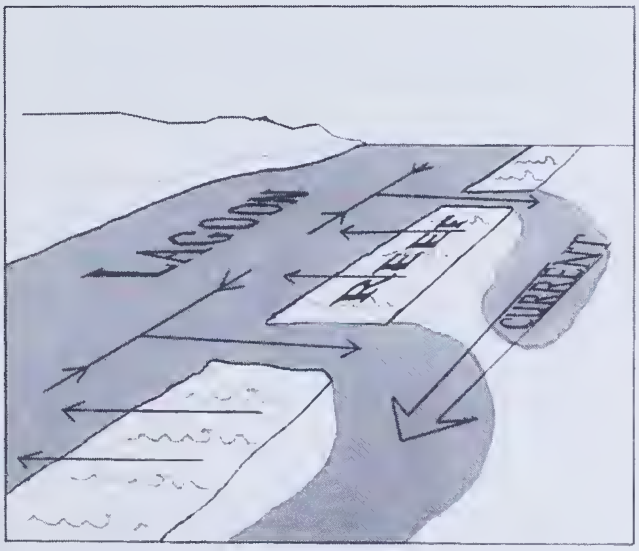

Figure 2. The Ningaloo Reef is a classic fringing reef, with a shallow lagoon. Surf coming over the reef brings a torrent of richly oxygenated water into the lagoon which returns to the open ocean via gaps in the reef. This turbid green-coloured water flowing through gaps in the reef can clearly be seen, particularly from the air. It is taken north or south along the reef front by the prevailing reef front current.

aircraft flying over the reef at a height of 370 m. For the purpose of assessing the prevailing current, the reef was divided into three sections (Fig 1); Tantabiddi to Yardie Creek, Yardie Creek to Point Cloates (Ningaloo Station), and Point Cloates to Coral Bay (this third section was only surveyed in 1991). The surveys were at about weekly intervals between February and May (Table 2). They were more intensive in 1991 with both morning and afternoon observations; in 1990 and 1992 extra flights were conducted.

On 11 April 1991, a Platform Transmitter Terminal (PTT) for satellite tracking utilising the ARGOS system, became detached from a whale shark off Tantabiddi at the northern end of the reef. This unit, which had a keel extending 30 cm below the sea surface, effectively became a current drogue, giving additional information about the prevailing current. Current measurements using current meters on the outer continental shelf (Boland *et al.* 1988, D R Tippins & M Tomczak, Flinders Institute of Atmospheric and Marine Sciences, unpublished data, personal communication) are also reviewed to show the larger-scale circulation features in the Ningaloo area.

Sea-surface temperature (SST) images of the area were obtained from the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA satellites. These enable circulation patterns in the water to be inferred when there are water masses (currents) with different temperatures. For overhead passes, the pixel resolution is about 1 km, so features less than about 2 km from the coast cannot be assessed; because the satellite precesses daily, for part of the time Ningaloo is near the edge of the pass where the spatial resolution is of the order of 5 or 6 km. In 1991 water temperature measurements were available from a thermistor on board the vessel "Nordon" operating outside the northern reef from early March until the middle of April, allowing confirmation of the satellite-derived sea surface temperatures.

Table 2

Current observations from the aerial surveys. The wind and current direction was determined from observations on aerial surveys. A "-" denotes that no current was detectable, usually because of insufficient flow from the lagoon. Wind directions are (by tradition) *from* and current directions are *to*.

1990

Date	Wind Direction	Current direction
05-Feb	S	-
10-Mar	SW	-
16-Mar	S	S
20-Mar*	SW	N
26-Mar*	SW	N
28-Mar	SW	S
02-Apr	SW	N
10-Apr	S	S
16-Apr	N	S
14-May	SW	S

In 1990 aerial surveys were flown from the northern end of the Ningaloo tract as far as Fraser island off Ningaloo Station. Take-off was usually at 14:00. Two additional flights along the reef produced current data, on 20 March at 10:30 and on 26 March at 17:00 (*)

1991

Date	Wind Direction	Current direction (3 sectors)		
10 Feb pm	SW	-	N	-
28 Feb pm	SW	S	S	S
06 Mar pm	SW	N	N	N
14 Mar am	S	-	-	-
14 Mar pm	SW	-	-	-
20 Mar am	SW	-	-	-
20 Mar pm	SW	-	N	-
28 Mar am	-	-	-	-
28 Mar pm	-	-	N	-
05 Apr am	N/S	N	-	-
05 Apr pm	N/SW	S	N	-
12 Apr am	SW	-	-	N
12 Apr pm	SW	-	-	-
21 Apr am	N	N	N	N
21 Apr pm	N	N	N	N
28 Apr am	SW	-	-	-
28 Apr pm	SW	N	-	-
28 May am	S	-	-	-
28 May pm	S	-	-	-

In 1991 aerial surveys were conducted with morning take-offs (10:30) flying south to Coral Bay, returning in the afternoons (14:00 take-off). The current direction was assessed where possible in three sectors, the boundaries being Yardie Creek, Point Cloates and Coral Bay.

1992

Date	Wind Direction	Current direction (2 sectors)	
01-Mar	SW	N	N
14-Mar	SW	N	N
21-Mar	S	S	-
29-Mar	N	-	.
04-Apr	SW	N	N
08-Apr	SW	N	N
14-Apr	S	N	-
21-Apr	-/S	N	N
01-May	S	S	S
09-May	-	-	-
16-May	E	-	S
26-Jun	-	S	S
03-Aug	S	N	-

In 1992 survey flights were flown from the northern end of the reef south to Point Cloates at Ningaloo, with a 10:30 takeoff; the current was assessed in northern and southern sectors, to the north and south of Yardie Creek Gorge.

Results

Winds

The wind records from Cape Cuvier demonstrate the seasonal weather pattern experienced at Ningaloo (Fig 3). During much of the year, prevailing south-easterly trade winds during the night and morning are replaced by stronger south-westerly sea-breezes in the afternoon. The mean wind speed in summer is 7 to 9 m s^{-1}, but this falls to only about 3 m s^{-1} in winter due to the more variable wind directions in that season. Peak wind speeds exceed 14 m s^{-1} in all months. This pattern is essentially similar to that found by Hearn *et al.* (1986) at Carnarvon (25° S) and Learmonth (on the east coast of Exmouth peninsula), allowing for local effects at those two sites.

A strong and persistent southerly wind blows between about September and March, and by April the prevailing winds swing more to the east (particularly during the mornings), delaying the onset of the south-westerly sea-breeze and often giving a period of calm conditions in the middle of the day. In some years, large continental high pressure systems produce strong daytime north-easterly winds in May and June.

Coral spawning

The dates of coral spawning at Ningaloo between 1984 and 1996 are listed in Table 1. Observations collected from divers at different locations have suggested spawning is not necessarily uniform along the reef. In some years, northern reefs of Exmouth Gulf and at Tantabiddi tend to spawn more heavily early in March, whereas the southern reefs (Coral Bay) had heavy spawning in April. In 1992, for instance, there was heavy spawning in Exmouth Gulf on 26-27 March, and very little activity reported from Coral Bay. The second spawning on 24-25 April was very heavy in Coral Bay with formation of extensive slicks. This is the latest date of a heavy spawning yet observed by the authors.

Surface and aerial observations of currents

Preliminary direct observations of currents from boats between 1987 and 1989 suggested that the reef-front current is usually northward during March and early April, and only turns persistently southward during the second half of April. In 1987 for instance, the reef corals spawned on 21-22 March; on 28 March and 4 April there was clear evidence of a northward current, and it was not until 8 April that a southward current was first evident along the reef front.

Aerial surveys conducted from 1990 to 1992 confirmed the presence of the northward current, and also showed that March to April is a transition period from the summer to winter pattern. In 1990 (Table 2), no northward currents were seen after 2 April. In 1991 and 1992, a northward current predominated in March and April, still being evident on 28 April 1991 and 21 April 1992, well after the dates of coral spawning that year. The direction of the current was generally, but not always, the same as the wind on the reef front (*e.g.* southerly wind generating a northward current).

When the northward current was present along the reef front, it was often clear that the Leeuwin Current was strongly pushing southward some 2 km offshore. From the air, a definite line was evident on the water with comparatively calm water near the coast and rougher seas beyond as the southward current pushed against the northward winds (the "wind-versus-current" phenomenon). On calmer days, fingers of clear blue offshore water could be seen meeting the greener turbid water of the reef-front.

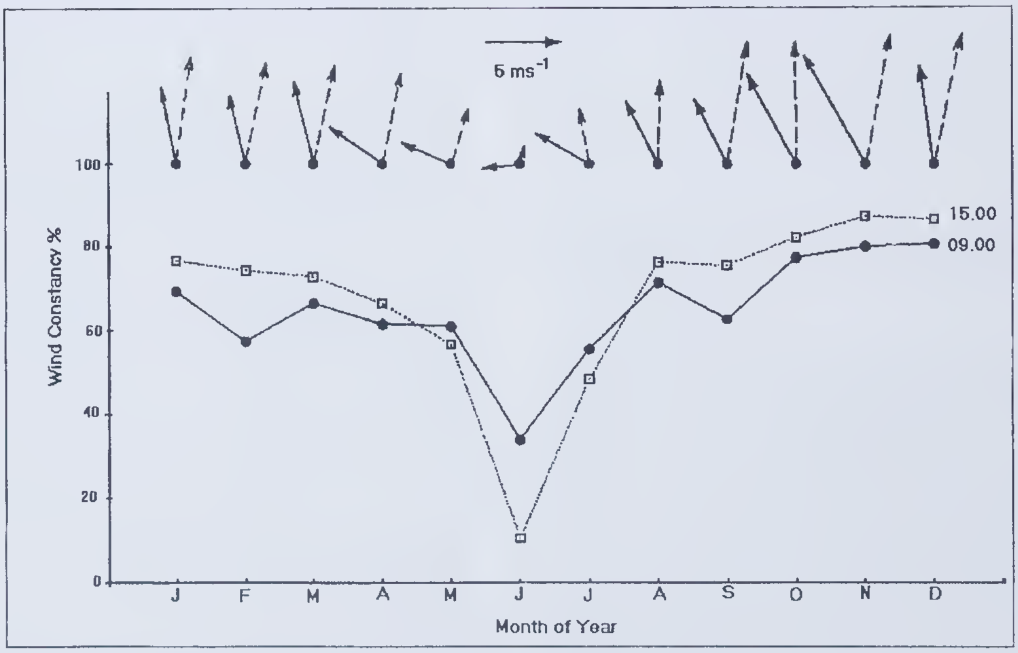

Figure 3. Monthly mean wind vectors at Cape Cuvier (24° 13' S, 113° 23' E) at 09.00 (solid arrows) and 15:00 (dashed), and wind "constancy" (a measure of the persistence of the wind direction) at 09.00 and 15.00 for 1972-75. Data are from the Bureau of Meteorology (Perth, Western Australia).

Satellite imagery of currents

The satellite images presented here are from 1991 and can be related to the data presented from the aerial surveys and the PTT current drogue (see below). Similar patterns have been observed in the subsequent years, 1992 to 1996.

The Leeuwin Current originates north of Exmouth, the satellite imagery often suggesting a "funnelling" of warm water from the north-west, north and north-east down towards the Exmouth region. On occasion, there is a south-westward flow along the Northwest Shelf (as described by Holloway & Nye 1985), but many images also indicate a near-zonal front at the latitude of Northwest Cape, indicating a strong eastward flow towards the Ningaloo Reef, the Eastern Gyral Current described by Wijffels (CSIRO Marine Research, Hobart, personal communication). These sources merge and deflect southwards as the Leeuwin Current, but with considerable spatial and temporal variability. The Leeuwin Current generally therefore becomes identifiable as a boundary current in the Exmouth/Ningaloo area, but is not always well-defined along this section of the coast, particularly during the summer months. As shown by Smith *et al.* (1991), the southward transport of the Leeuwin Current increases south of Shark Bay, and temperatures derived from satellite imagery indicate that the surface thermal contrast between the Leeuwin Current and the cooler offshore water also increases with latitude southwards.

The warm Leeuwin Current and the cool counter-current are visible in many summer/autumn images, particularly south of Point Cloates where the shelf is wide, although further north the inshore current is very narrow and sometimes at the limit of resolution. Further, surface temperature gradients across the Leeuwin Current are weaker during summer than in winter when the current is flowing strongly, so the flow is not always clearly defined in summer images. Nevertheless, the NOAA/AVHRR satellite images depict sea-surface temperatures from which the larger-scale features of the ocean circulation off the Ningaloo Reef can generally be deduced.

As off the south-west coast (Pearce & Pattiaratchi 1999), when the southerly wind stress is very strong during the summer months, the Leeuwin Current weakens and becomes less clearly defined. It tends to move further offshore and a coastal current of cooler water flows northwards from (at least) the southern end of the Ningaloo Tract towards Point Cloates and continues along the reef front. It may be narrow and restricted to the inner shelf (Fig 4A) or can extend well across the shelf and upper slope (Fig 4B,C). Many images show the counter-current continuing eastwards past North-West Cape and the Muiron Islands. In contrast,

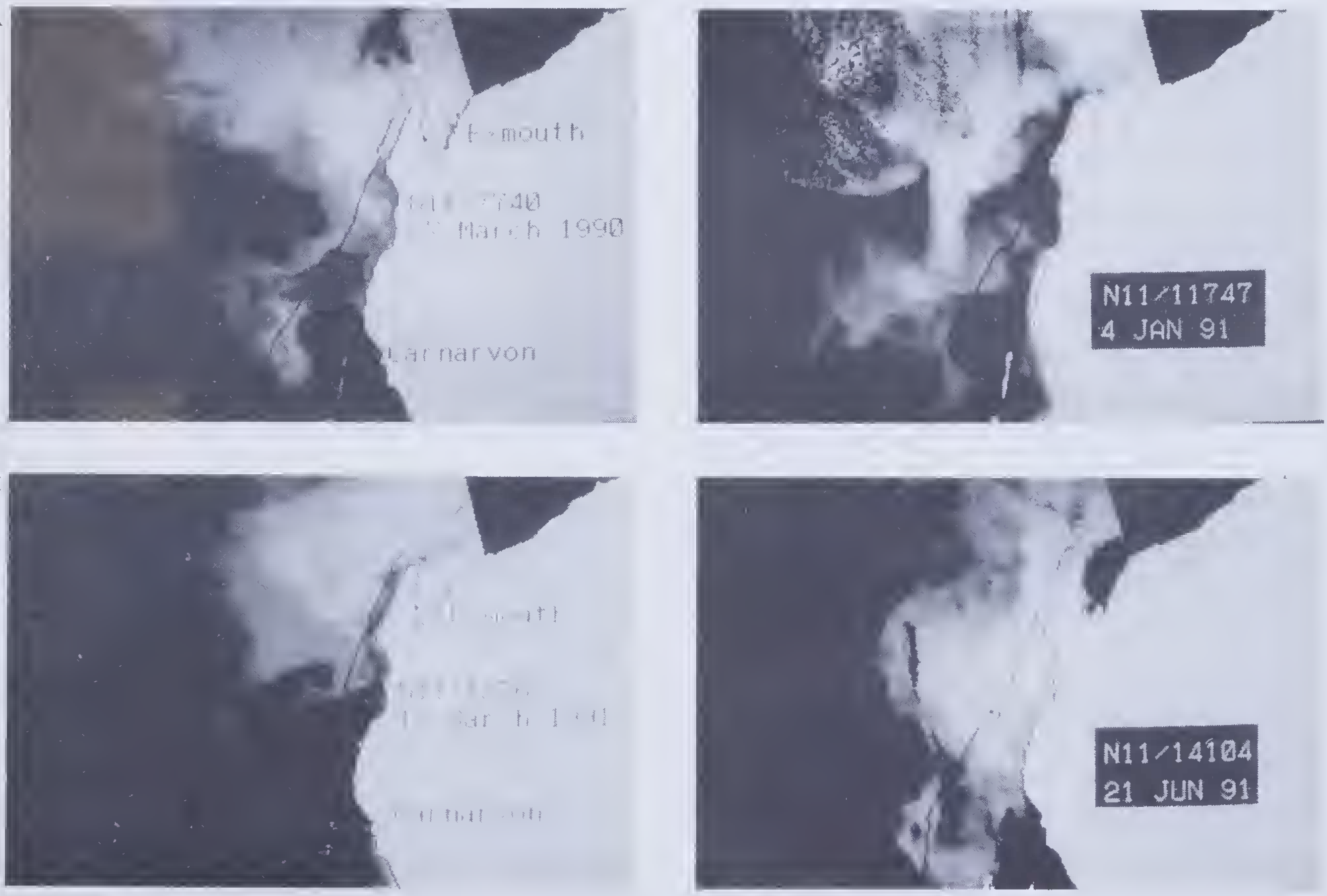

Figure 4. NOAA-AVHRR images of the Ningaloo area in (A) March 1990, (B) January 1991, (C) March 1991 and (D) June 1991. Warmest water is shown in palest shades of grey and coolest water in dark shades. The black line depicts the edge of the continental shelf. Each image shows the brightness temperature in the AVHRR Band 4 (*i.e.* uncorrected for atmospheric effects, and so are likely to be between 1° and 3° cooler than the true surface temperatures). Each image has been enhanced to show specific current details, so there is no particular connection between the temperature/colour scales between the images.

during the winter months when the net southerly winds are relatively weak (Fig 3), the Leeuwin Current flows southward along the continental shelf, spreading across the shelf to the coast and also floods into the bight south of Ningaloo Station (Fig 4D).

A feature of many summer images is an anti-clockwise eddy peeling from the Leeuwin Current and penetrating across the shelf towards the coast in the bight south of Point Cloates and presumably joining the counter-current (Fig 4A,B,C). The significance of this (topographically-induced?) eddy is that it represents a possible mechanism for any biota such as zooplankton or coral spawn which may mix across the shelf into the Leeuwin Current from the northern Ningaloo Reef to re-circulate back into the coastal system via the northward countercurrent.

Sea-surface temperatures on the open continental shelf off Ningaloo range from about 27° C between February and April to 22° C in August/September (Marine Climatic Atlas of the World, CD-ROM, US Naval Oceanography Command, Ashville, NC). Boat measurements of water temperature were available in March 1991 confirming the impression from aerial and satellite data. The turbid "green" water on the reef front was repeatedly measured at 26.3 °C to 26.5 °C with a sharp rise in temperature to 27.1 °C on crossing into the clear oceanic water offshore.

Current drogue trajectory

On 11 April 1991, four days after a coral spawning event, the ARGOS satellite PTT, which detached from a whale shark close to the northern end of the reef, was taken south for most of the period it was tracked in the Leeuwin Current, against the strong southerly winds normally prevailing at that time of year (Fig 3), indicating that the "windage" was relatively small. However, it was initially carried north and circled in an eddy off North-West Cape for nearly two days before being taken rapidly south (at up to 45 cm s^{-1}, or almost a knot) in the Leeuwin Current (Fig 5). On 18-19 April it was brought closer inshore by an anti-clockwise eddy or current meander off Coral Bay and then travelled north for two days before being taken south again towards Cape Cuvier. This trajectory showed the reef front current flowing northwards (off North-West Cape and off Coral Bay) and the Leeuwin current flowing strongly southwards offshore, as well as indicating some degree of cross-shelf exchange/recirculation of water. A satellite image for 4 April that year clearly shows an anti-clockwise eddy near Coral Bay and the counter-current running northwards along the Ningaloo reef (Fig 6).

Current meters

Near-bottom currents at the shelf-break were measured by CSIRO during the Leeuwin Current Interdisciplinary Experiment (LUCIE) between September 1986 and August 1987. The current meter was 15 m above the seabed in 118 m water depth (Boland *et al.* 1988). Although the mooring may not have been in the strongest part of the Current, the flow was southward at between 10 and 40 cm s^{-1} for almost the entire year, with strongest currents (up to 60 cm s^{-1}) in May and June.

Measurements from a current meter further down the continental slope between 1994 and 1996 also indicated a predominantly southward flow (strongest from February to April) with sporadic reversals between August and October when the Leeuwin Current had weakened (D R Tippins & M Tomczak, Flinders Institute of Atmospheric and Marine Sciences, personal communication). Peak near-surface current speeds were of order 1 m sec^{-1}, and below about 150 m depth there was a northwards counter-current as found earlier by Thompson (1984).

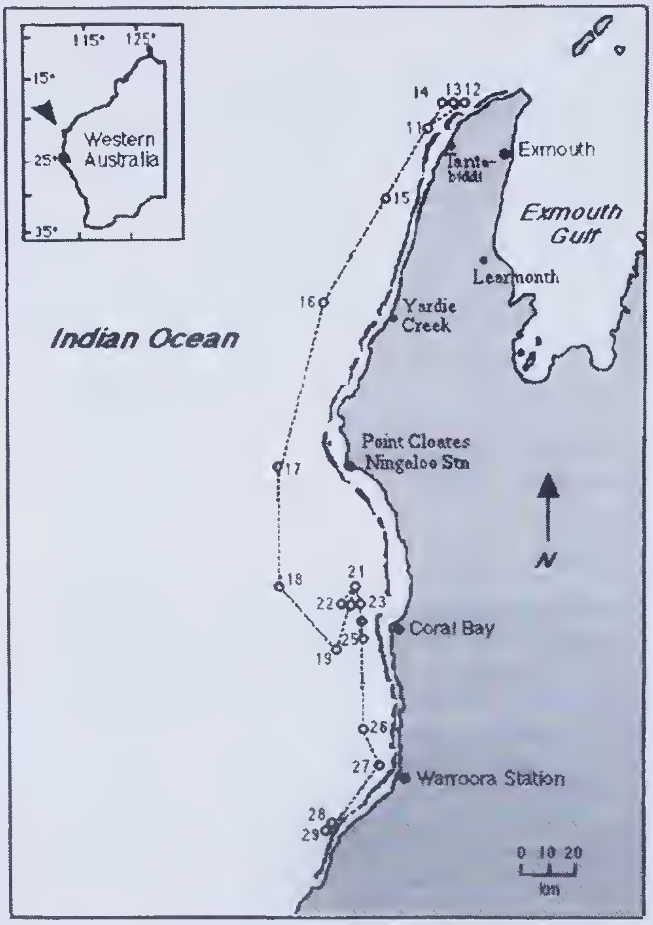

Figure 5. The trajectory of a satellite PTT transmitter which had become detached from a whale shark in April 1991, effectively acting as a current drogue. The date of each daily position (the first fix of the day, usually 0600 to 0700 GMT) is shown next to each point.

Figure 6. NOAA-AVHRR image of the Ningaloo area in April 1991 clearly showing the counter-clockwise eddy south of Coral Bay, and the northward current on the wide shelf south of Point Cloates. Other details as in Fig 4.

Discussion

The preliminary observations made in autumn each year at Ningaloo showed that a northward cool coastal current flowed during March and early April, the period of the annual mass spawning of corals. The observations made on the water and from aircraft were confirmed by studying the satellite imagery from the same period. More extensive studies of the satellite imagery then showed that the northward flowing current is predominent for the majority of the year (8 months). It should be appreciated that the images presented in this paper are a small sample of the many images studied.

The northward counter-current predominates on the reef-front from September through the summer till mid-April, and is thought to be largely driven by the South-East (Trade) winds and the strong diurnal coastal south-westerly sea-breezes (Fig 3). We propose that this current should be called the "Ningaloo Current". In the southern reef where the continental shelf is wide, the current is broad based, up to 30 km wide, and more easily seen on satellite imagery. To the north of Point Cloates where the seabed shelves more rapidly, the northward current is often less than 2 km in width, and at times too narrow for resolution by satellite imagery.

The cold water temperature anomalies observed by Simpson & Masini (1986) have given rise to speculation regarding upwelling at Ningaloo. There has been no convincing evidence of upwelling from the satellite imagery. However, the counter-current model gives a possible explanation of how the anomalies might occur. The Ningaloo Current is a cool current and the temperature of water travelling north will depend on the degree of mixing with the warmer Leeuwin Current offshore, and the amount of recirculation caused by eddies such as the one observed off Coral Bay. Indeed, this eddy demonstrates how upwelled water masses from offshore might be advected to the reef front. Hearn *et al.* (1986) were concerned that large temperature gradients would be required to produce such an anomaly. However, in the field, a gradient of 0.5 °C in a few metres has been measured between different water masses off Tantabiddi.

The initial observations were made in autumn at the time of transition from the summer to winter pattern. The timing of this transition varies from year to year depending on weather conditions, and may be critical to biological processes in the region. The northward alongshore flow acts as a counter-current to the Leeuwin Current, and sometimes extends eastwards past North-West Cape. These opposing currents generate a re-circulation of water in the region. To the north of the Cape there are strong tidal influences produced by the ebb and flow of tides in Exmouth Gulf. Further south the prominence of Point Cloates is conducive to the formation of a topographic eddy in the Leeuwin Current which has been observed on many satellite images, bringing warm water into the southern end of the Ningaloo Reef tract.

The presence of the Ningaloo Current and this circulatory movement of water has major implications for various biological systems in the region. Scientists have long argued about the enigma represented by the high productivity of coral reefs existing in waters that are low in essential nutrients such as phosphate and nitrogen (Hatcher 1988; Kinsey 1991). The production of spawn by the coral is a major annual event of lipid and protein production, so the mass spawning of a coral reef represents a significant export of protein, and therefore nitrogen, from the reef itself.

Theories regarding coral spawn dispersal at Ningaloo have hitherto assumed that the spawn from the Ningaloo Reef is carried south by the strong Leeuwin Current (Simpson 1985, 1991) as a unidirectional flow of genetic material. Our observations in the field over the period of this study have shown that the reef front current is in fact northward during at least the March spawning and usually during the April spawning as well, especially if this occurs early in the month. The track of the PTT current drogue demonstrates the situation in 1991. It was deployed on 11 April, after the coral had spawned on 7-8 April, and clearly demonstates a likely pattern for the dispersal of coral spawn that year. The drogue was eventually brought inshore towards the reef and travelled northward off Coral Bay. We suggest that the nearshore counter-current system observed at Ningaloo during the period of the annual mass spawning is responsible for maintaining a large proportion of the exported protein within the Ningaloo Reef system and may therefore be important for the survival of the reef itself.

Many other marine organisms apart from the coral spawn at this time of year. One example is the mass epitokous spawning of polychaete worms which occurs synchronously with the corals. It has been proposed that this mass spawning releases large amounts of protein into the waters of the region, boosting the zooplankton food

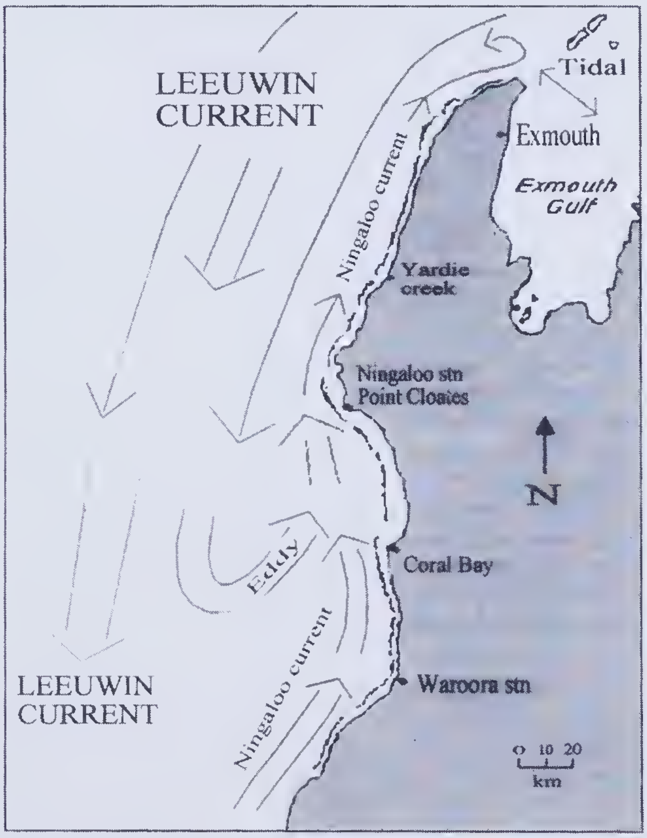

Figure 7. Proposed current mechanisms at Ningaloo Reef operating principally from September until mid-April.

chain at this time of year (Taylor 1989, 1996). There are likely to be inter-annual variations in the strength and transport of the counter-current, largely resulting from variability in the winds and in the strength and position of the Leeuwin Current, and the productivity of the area may accordingly be affected. The abundance of filter-feeding marine animals such as the whale shark (*Rhincodon typus*) may reflect the abundance of zooplankton in the area. Indeed, the presence of whale sharks could be looked upon as an indicator of zooplankton abundance.

The first observations of a whale shark surface-feeding during the day at Ningaloo were made in March 1991, 14 days after the March coral spawning. A strong northerly current was sweeping huge swarms of spawning krill *Pseudeuphausia latifrons* along the reef-front. The whale shark charged through the swarms of krill with its mouth agape, trapping its prey against the water surface; this surface feeding behaviour is more common at dusk (Taylor 1994).

Studies of whale sharks at Ningaloo are incomplete, having concentrated mainly on the northern reef, north of Point Cloates (Taylor 1989, 1994, 1996). The area was studied in greater detail with aerial surveys from 1990 to 1992. The surveys showed that while the sharks may be spread all along the reef in the early part of the season, they would aggregate into one area, during April. This aggregation is usually along the northern reef, close to Tantabiddi, but in 1989 it was further south off Yardie Creek, and in 1990 no aggregation was found at all in the northern reef area (Taylor 1996). These data suggest some correlation between the presence of the northerly counter-current and the abundance of whale sharks at the northern end of the reef. April 1990 was a season of very low whale shark sightings; the reef front current during April was predominantly southwards (Table 2). During the following two years, 1991 and 1992, when the aerial surveys showed good evidence of the northerly counter-current throughout April, large numbers of whale sharks were encountered (Taylor 1996). More recently, 1995 was a relatively poor whale shark season with low numbers of encounters reported by commercial operators; it was also a year of unseasonal calm, humid weather and direct observation showed no evidence of a northward current on the reef front in early April, with a strong southward current noted by the 8-9 April.

The 1998 whale shark season had very low numbers in the northern reef area, similar to 1990. A coastal trough formed in March and persisted into April, bringing calm sea conditions and early rain. The south-westerly sea-breeze was weak or absent throughout that period, and satellite images show little evidence of either Leeuwin or Ningaloo Currents. Sea temperatures on the reef front were greater than 29 °C, which is 2 °C hotter than any previous year and consistent with the absence of the cool Ningaloo current.

Our observations show that the northward counter-current is well established during the summer months with the strong southerly winds. April is a month of transition to the winter pattern, and in early winter, when north-easterly winds are common, the southward Leeuwin current predominates. In June 1993, much publicity was given to the "fish feeding frenzy" at Cape Cuvier, to the south of the Ningaloo Tract, where sharks and Bryde's whales were seen feeding on huge schools of anchovies. It may be relevant that on 19 May that year, a massive school of anchovies estimated at one kilometre in diameter was reported by charter boats and aircraft off the northern Ningaloo Reef at Tantabiddi (Fig 1). The school was surrounded by sharks, manta rays and whale sharks. It is possible that this was the same fish school, taken south by the Leeuwin current, as the one seen the following month beneath the cliffs at Cape Cuvier. Based on the current drogue observations it would take 10 days (at a speed of 20 cm s^{-1}) for such a fish school to be taken south to Cape Cuvier. It can be seen that the high productivity of the Ningaloo tract in the autumn is eventually dispersed southwards by the Leeuwin current during the winter months, and may affect the productivity of the whole west coast. A second satellite PTT was deployed in March 1991 but malfunctioned; it was recovered from a beach at Lancelin (100 km north of Perth) only 4 months later, representing a southwards transport of order 10 cm s^{-1}, which compares well with current estimates by Hutchins & Pearce (1991).

Comparing the Ningaloo and Barrier Reefs, Simpson (1991) proposed that the natural selection of corals that spawn at this time of year on the west coast of Australia reflects historical breeding patterns, and are a result of ocean currents emanating from the Indonesian Archipelago. The strong Leeuwin Current brings autumn spawners down the west coast, while spring spawners are taken eastwards to the Great Barrier Reef. Extrapolating from this theory, natural selection may also operate at a more local level. Organisms that spawn when the Leeuwin Current flows strongly on the reef front would have their progeny moved progressively southwards, and could only survive on the reef through replacement from further north (Simpson 1991). During the period that the counter-current operates, however, spawn may be maintained within the reef system allowing local settlement to occur. Organisms, and in particular corals, that spawn when the counter-current is operating would be more likely to survive on the reef. Hence, it is possible that the counter-current system through natural selection may influence the timing of the reef spawning.

We suggest that there are 3 current zones across the continental shelf off Ningaloo (Fig 7); the warm southward Leeuwin Current, flowing along the outer shelf/upper slope and driven by an alongshore pressure gradient (Godfrey & Ridgway 1985); a seasonal wind-driven northward inner-shelf counter-current, the Ningaloo Current (this study); and a wave/wind/tidally-driven flow within the nearshore reef system (Hearn *et al.* 1986). With the present interest in the Cape Range Peninsula of the oil industry, the area could in the future see the establishment of off-shore oil tanker terminals. It is therefore of vital importance that a full understanding of current mechanisms at Ningaloo is developed to assist the industry in oil spill contingency planning.

Acknowledgements: Satellite imagery was acquired from the Western Australian Satellite Technology and Applications Consortium (WASTAC), and wind data for Cape Cuvier were provided by A Scott (Bureau of Meteorology). B Mate and S Nieukirk assisted with Argos data collection. Thanks also to P Arscott, the pilots of Exmouth Air Charters, and the observers who assisted in the aerial surveys. This study was partially supported by the Fisheries Research and Development Corporation (FRDC).

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